

A Survey of the Lace-necked Dove in Hawaii

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Streptopelia chinensis chinensis (Scopoli), popularly called the Lace-necked or Spotted Dove because of its characteristic feather pattern, is a common member of the introduced avifauna of the Hawaiian Islands. No information is available concerning the date or exact source of its importation from eastern China to Hawaii, but this dove was very common on Oahu in 1879 (Caum, 1933) and had become established on the other major islands sometime prior to 1900 according to long-time residents interviewed during this survey.

Lace-necked Doves are now permanent residents on all the major Hawaiian Islands. Kahoolawe, a 45-square-mile bombing target under military jurisdiction and 6½ miles offshore from Maui, was not visited during this survey but it is likely that Lace-necked Doves live there. No personal observations were made on Niihau, but the owners of this 72-square-mile island reported in conversation that Lace-necked Doves were well established there and this report has been confirmed by Fisher (MS). The Lace-necked Dove has been observed to fly between the islands of Niihau and Kauai, a distance of 18 miles, and it is conceivable that this species may have voluntarily established itself on the major islands other than Oahu, the probable site of original planting. If this is so, the greatest flight over open water would have occurred between Oahu and Kauai, a distance of 73 miles. The alternative of transportation from one island to another by humans is likewise plausible.

DISTRIBUTION AND POPULATION

Climatic conditions and the vegetative pattern define the limits of the range of the Lace-necked Dove in the Hawaiian Islands and influence the use of a given area and its population density. The range of this species occurs mostly from sea level to 4,000 feet elevation (Fig. 2), where mean annual temperatures grade from 75° F. at the lowest elevation to 60° F. at the highest elevation; however, in one area on Hawaii it reaches 8,000 feet, where the mean annual temperature is estimated to be around 40° F. Depending on the locality, rainfall in the Hawaiian range of this species varies from less than 10 inches up to a maximum of 250 inches annually. Lace-necked Doves are found in pineapple and sugar cane plantations, in pastures and waste lands, in small truck gardens, homesteads, and urban areas, and in openings of forested sections; dense forests and barren lava are uninhabited.

In order to evaluate this distribution and the abundance of Lace-necked Doves, we have employed the classification of *Vegetation Zones of Hawaii* (Ripperton and Hosaka, 1942), which correlates climatic conditions, the vegetation pattern, and land use throughout Hawaii. While these zones are referred to here, their descriptions and maps are not repeated because of summaries in two other publications (Schwartz and Schwartz, 1949 and 1950).

Range, populations, and densities of the Lace-necked Dove are given according to vegetation zone in Table 1. Strip counts were made in all occupied range and formed the basis for densities representing daytime dis-

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TABLE 1
DISTRIBUTION AND POPULATIONS OF THE LACE-NECKED DOVE IN HAWAII BY VEGETATION ZONE

VEGETATION ZONES	SQUARE MILES	SQUARE MILES OCCUPIED	PERCENTAGE OF ZONE OCCUPIED	TOTAL POPULATION	SQUARE MILES WITH DENSITIES OF				
					1-10	11-25	26-50	51-100	101-200
ZONE A									
Hawaii....	249	232	94	3,920	82	111	39	0	0
Kauai.....	23	23	100	1,150	0	0	23	0	0
Lanai.....	72	72	100	630	66	0	6	0	0
Maui.....	121	97	80	5,160	3	0	77	17	0
Molokai...	64	64	100	5,060	0	24	0	33	7
Oahu.....	67	51*	76	1,020	0	51	0	0	0
Total....	596	539	90	16,940	151	186	145	50	7
ZONE B									
Hawaii....	408	397	97	11,090	169	63	165	0	0
Kauai.....	116	113	97	3,850	0	60	53	0	0
Lanai.....	57	57	100	2,440	23	0	13	21	0
Maui.....	138	78	56	4,250	0	0	65	13	0
Molokai...	74	74	100	4,200	0	32	12	25	5
Oahu.....	169	137†	82	3,840	0	117	0	20	0
Total....	962	856	89	29,670	192	272	308	79	5
ZONE C ₁									
Hawaii....	194	183	94	2,940	96	79	8	0	0
Kauai.....	88	78	89	3,200	8	13	57	0	0
Lanai.....	10	9	90	400	4	0	2	3	0
Maui.....	54	37	68	1,710	0	5	32	0	0
Molokai...	46	44	96	4,330	0	9	0	28	7
Oahu.....	146	132	90	3,550	0	106	13	13	0
Total....	538	483	90	16,130	108	212	112	44	7
ZONE C ₂									
Hawaii....	316	196	62	5,740	70	42	84	0	0
Kauai.....	11	10	91	190	1	9	0	0	0
Lanai.....	0	0	0	0	0	0	0	0	0
Maui.....	61	34	56	2,550	0	0	0	34	0
Molokai...	0	0	0	0	0	0	0	0	0
Oahu.....	0	0	0	0	0	0	0	0	0
Total....	388	240	62	8,480	71	51	84	34	0
ZONE D ₁									
Hawaii....	464	417	90	4,880	346	71	0	0	0
Kauai.....	113	73	65	1,950	2	54	17	0	0
Lanai.....	2	0	0	0	0	0	0	0	0
Maui.....	97	69	71	2,810	16	0	53	0	0
Molokai...	32	2	6	400	0	0	0	0	2
Oahu.....	110	101	92	3,440	0	54	29	18	0
Total....	818	662	81	13,480	364	179	99	18	2
ZONE D ₂									
Hawaii....	790	104	13	1,040	104	0	0	0	0
Kauai.....	194	0	0	0	0	0	0	0	0
Lanai.....	0	0	0	0	0	0	0	0	0
Maui.....	151	5	3	250	0	0	5	0	0
Molokai...	44	0	0	0	0	0	0	0	0
Oahu.....	112	30	27	600	0	30	0	0	0
Total....	1,291	139	11	1,890	104	30	5	0	0

*Sixteen square miles of urban area occupied by Lace-necked Doves not censused.

†Thirty-two square miles of urban area occupied by Lace-necked Doves not censused.

TABLE 1 (Continued)
DISTRIBUTION AND POPULATIONS OF THE LACE-NECKED DOVE IN HAWAII BY VEGETATION ZONE

VEGETATION ZONES	SQUARE MILES	SQUARE MILES OCCUPIED	PERCENTAGE OF ZONE OCCUPIED	TOTAL POPULATION	SQUARE MILES WITH DENSITIES OF				
					1-10	11-25	26-50	51-100	101-200
ZONE D ₃									
Hawaii	353	74	21	740	74	0	0	0	0
Kauai	10	9	90	130	4	5	0	0	0
Lanai	0	0	0	0	0	0	0	0	0
Maui	23	0	0	0	0	0	0	0	0
Molokai	0	0	0	0	0	0	0	0	0
Oahu	0	0	0	0	0	0	0	0	0
Total	386	83	21	870	78	5	0	0	0
ZONE E ₁									
Hawaii	647	92	14	940	90	2	0	0	0
Kauai	0	0	0	0	0	0	0	0	0
Lanai	0	0	0	0	0	0	0	0	0
Maui	39	0	0	0	0	0	0	0	0
Molokai	0	0	0	0	0	0	0	0	0
Oahu	0	0	0	0	0	0	0	0	0
Total	686	92	13	940	90	2	0	0	0
ZONE E ₂									
Hawaii	503	28	5	280	28	0	0	0	0
Kauai	0	0	0	0	0	0	0	0	0
Lanai	0	0	0	0	0	0	0	0	0
Maui	44	0	0	0	0	0	0	0	0
Molokai	0	0	0	0	0	0	0	0	0
Oahu	0	0	0	0	0	0	0	0	0
Total	547	28	5	280	28	0	0	0	0
ZONE E ₃ No Lace-necked Doves									
TOTALS									
Hawaii	4,030	1,723	43	31,570	1,059	368	296	0	0
Kauai	555	306	55	10,470	15	141	150	0	0
Lanai	141	138	98	3,470	93	0	21	24	0
Maui	728	320	44	16,730	19	5	232	64	0
Molokai	260	184	71	13,990	0	65	12	86	21
Oahu	604	451	75	12,450	0	358	42	51	0
Total	6,318	3,122	49	88,680	1,186	937	753	225	21

tribution. These were made in conjunction with inventories taken of other game birds and offered us the most suitable means for establishing satisfactory estimates of population densities. It is realized that a daytime population estimate may include some birds feeding but not roosting in a given zone. However, in the overall population estimate, any error due to this fact appears to be of little consequence. Much of the daily movement takes place within a vegetation zone, and where flyways do exist, they are generally

found between vegetation zones A, B, and C₁, all of which rank as dove range of equal quality on the basis of strip-count estimates. Field observations on the amount of available dove food and the occurrence of roosting cover correspond to the general ratings of vegetation zones by population estimates. An analysis of Table 1 shows zones A, B, and C₁ to be the best zones for Lace-necked Doves. They all have high percentages of occupancy (89-90 per cent), high populations (16,000-29,000), and include very high



FIG. 1. Adult Lace-necked Dove. Waikii, Hawaii. Elevation 4,700 feet above sea level; April 5, 1946.

densities (up to 200 birds per square mile). These zones occupy the coastal regions below 2,500 feet elevation, where mean temperatures are between 75° and 70° F. annually and where rainfall varies from less than 10 to approximately 60 inches annually. The densest populations in these zones occur on Molokai and are the result of a desirable combination of habitat requirements. One of the most productive areas centers in the region of pineapple cultivation near Hoolehua. A resident population of doves utilizes densely wooded draws and gullies for roosting areas, and forages in old pineapple fields rich in weedy growth and in fallow grain fields and garden plots of adjacent homestead areas. Water is obtained from the fruit of popolo (*Solanum nodiflorum*), scattered livestock watering places, and occasional rain

and dew. Two other regions of dove concentration on this island are found in the coastal flats and in areas immediately adjacent. Here, in the excellent roosting sites afforded by algaroba (*Prosopis chilensis*) are numerous stock watering units and some springs. On the adjacent dry open slopes, xerophilous plants such as uhaloa (*Waltheria americana*) and ilima (*Sida* sp.) produce an abundant seed crop utilized by these doves. Between these areas and the Hoolehua area there is considerable exchange of birds, which results in definite flyways.

Zones C₂ and D₁ are classed as intermediate dove range because of an intermediate percentage of occupancy (62–81 per cent), intermediate population (8,000–13,000), and intermediate densities (generally up to 100 birds per square mile). In these zones,

DISTRIBUTION AND DENSITY OF THE LACE-NECKED DOVE IN HAWAII

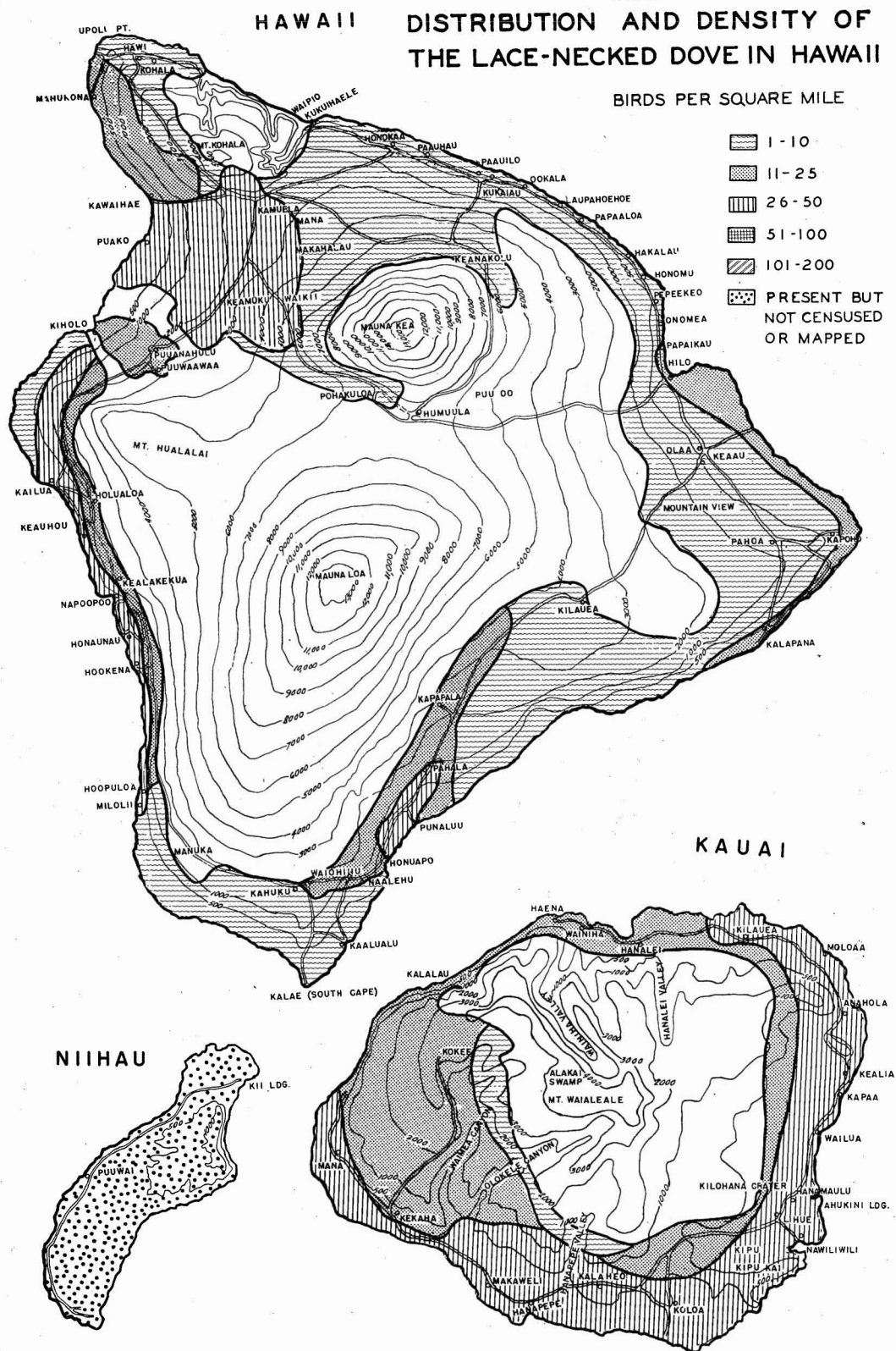




FIG. 3. Adult Lace-necked Dove. Waikii, Hawaii. Elevation 4,700 feet above sea level; April 5, 1946.

abundant food, available either seasonally or locally, is primarily responsible for the best densities, but the possible factors believed to limit high dove populations are different for the two zones. Zone C_2 lies between 2,500 and 4,000 feet elevation, where the annual mean temperature is 60° F. and the average rainfall is between 40 and 60 inches annually. This temperature is lower than those in the best Lace-necked Dove zones and is suggested as possibly being able to inhibit high populations. Zone D_1 , occurring between sea level and approximately 1,500 feet elevation, has an annual mean temperature of about 73° F. and an annual rainfall with a minimum of 60 inches. It is probable that the numerous and often heavy rains affect nesting success in this zone.

The poorest dove ranges occur in zones D_2 , D_3 , E_1 , and E_2 , which show low percentages of occupancy (5–21 per cent), poor populations (280–1,800), and generally low densities (50 or fewer birds per square mile). Zone D_2 lies between the general elevations

of 1,500 and 4,000 feet, where the annual mean temperature is 60° F. and rainfall reaches 450 or more inches annually. Low temperatures, heavy rainfall, and the lush forest cover all prohibit high densities. Doves are found only where suitable foods occur in small openings cleared for cultivation or resulting from heavy grazing. The other three zones, D_3 , E_1 , and E_2 , are above 4,000 feet elevation, where mean temperatures vary between 50° and 40° F. annually, and the extremes of rainfall are from about 100 inches at lower elevations to less than 40 inches at higher elevations. The cold temperatures probably contribute largely to the prevailing poor densities, but at lower elevations (D_3) the heavy rainfall is another adverse factor. Dove foods are extremely limited in these zones and water is unavailable in E_1 and E_2 .

Nearly all informed persons interviewed during this survey expressed the opinion that Lace-necked Doves have been decreasing in recent years. Many believe that competition for food between this species and the more plentiful and more recently introduced Barred Dove, *Geopelia striata striata* (L.), is the cause of this decrease but data from our food studies given below indicate otherwise. It may be significant that on Hawaii, where the Barred Dove is just becoming established in only a few localized areas, the same island-wide decrease of the Lace-necked Dove is also reported.

FOODS

An analysis was made of Lace-necked Dove foods from 146 crops and 71 gizzards. Each food species in the crop was identified, separated, measured in cubic centimeters, totaled by aggregate volume, and recorded for occurrence. Gizzard contents were identified and recorded for occurrence only. Every month except January and all islands except Niihau and Kahoolawe were represented in the sample. Except for four doves, all were collected between sea level and 2,700 feet elevation in zones A, B, C_1 , C_2 , and D_1 , and



FIG. 4. Lace-necked Doves frequently feed in the fallow sections (foreground) of pineapple fields which support a rich growth of herbaceous annuals. The cultivated pineapple fields (background) are seldom utilized by this species. Lanai. Vegetation zone B, elevation 1,500 feet above sea level; August 27, 1946.

from the distribution of the food species in the Islands, it was obvious that feeding occurred almost entirely within this area. No great seasonal difference occurs in the food supply of doves in Hawaii although there may be periods when individual plant species produce seeds more abundantly, especially following rains in the drier regions. This food analysis was not made according to vegetation zone, as was done for most other game birds during this survey, for two reasons: Some doves collected on flyways were suspected of having fed in a vegetation zone different from the one in which they were taken; also, only a few zones which comprise dove range in the lower elevations are used in this food analysis.

Table 2 lists the foods of the Lace-necked Dove in Hawaii. Sixty-five plant species form 99.5 per cent of the diet and 13 animal items constitute the remaining 0.5 per cent. Of the plant foods, seeds and pods form 84.1 per cent, succulent fruits constitute 14.4 per cent, and roots and seedlings comprise the remaining 1.0 per cent. The nine most important foods on the basis of volume and frequency of occurrence in crops (more than 2 per cent or more than 14 occurrences) are discussed briefly.

Momordica Balsamina L., balsam apple, is an exotic member of the family Cucurbitaceae and forms 23 per cent of the foods taken. It occurred in 43 (29 per cent) of the crops and 16 (22 per cent) of the gizzards. Although its

TABLE 2
FOODS OF THE LACE-NECKED DOVE IN HAWAII

SPECIES AND PARTS EATEN	PER-CENTAGE CROP VOLUME	NUMBER OCCURRENCES IN 146 CROPS	NUMBER OCCURRENCES IN 71 GIZARDS	ABUNDANCE OF FOOD BY VEGETATION ZONE*								
				A	B	C ₁	C ₂	D ₁	D ₂	D ₃	E ₁	E ₂
PLANTS	99.5											
<i>Momordica Balsamina</i> , balsam apple; seed	23.1	43	16		o	o						
<i>Waltheria americana</i> , uhaloa; seed	17.6	57	27	o	c	c	o					
<i>Cajanus Cajan</i> , pigeon pea; seed	12.8	21	4		r	o	r	r				
<i>Solanum nodiflorum</i> , popolo; fruit, seed	10.0	19	11		o	c		o				
<i>Lantana Camara</i> , lantana; fruit, seed	9.6	7	7	o	a	c		o				
<i>Wikstroemia phillyraefolia</i> , akia; fruit, seed	4.4	5	3		r	o						
<i>Portulaca sclerocarpa</i> , ihimakole; seed, pod	3.7	17	0		r							
<i>Dianella sandwicensis</i> , ukiuki; fruit, seed	3.1	1	1					o	o			
<i>Sida</i> sp. (<i>cordifolia</i>), ilima; seed and	2.9	32	10	o	c	r						
<i>Sida</i> sp. (<i>fallax</i>), ilima; seed †				c	a	c						
<i>Hordeum vulgare</i> , barley; seed	1.9	1	1				r					
<i>Centaurea melitensis</i> , Maltese thistle; seed	1.3	7	3	o	o							
Unidentified seeds	1.1	16	6									
<i>Euphorbia hypericifolia</i> , graceful spurge; seed	0.9	5	4		o	o						
<i>Grevillea robusta</i> , silk oak; seed	0.9	3	3		o	c						
<i>Ananas comosus</i> , pineapple; root	0.9	3	1		cultivated							
<i>Zea mays</i> , corn; seed	0.8	4	1		cultivated							
<i>Aleurites moluccana</i> , kukui; seed	0.7	1	1			o		c	c			
<i>Verbena litoralis</i> , verbena; seed	0.7	2	2		o	c	c				c	
<i>Phytolacca octandra</i> , pokeberry; fruit	0.4	4	5		r	r						
<i>Atriplex semibaccata</i> , Australian salt bush; seed	0.4	4	2	c	r							
<i>Euphorbia geniculata</i> , wild euphorbia; seed	0.3	1	1			o	o					
<i>Opuntia megacantha</i> , panini or cactus; seed	0.3	2	4	o	c	o						
<i>Prosopis chilensis</i> , algaroba or kiawe; seed pod, seedling	0.3	3	2	a	c							
<i>Sida rhombifolia</i> , ilima; seed	0.3	8	5		o	r						
<i>Euphorbia hirta</i> , garden spurge; seed	0.2	4	1		o	c						
<i>Avena fatua</i> , wild oat; seed	0.1	1	0		r	r	c					
<i>Carica papaya</i> , papaya; seed	0.1	1	0		cultivated							
<i>Eugenia Cumini</i> , Java plum; fruit	0.1	2	1		o	o		o				
<i>Portulaca cyanosperma</i> , small pigweed; seed	0.1	1	1	c								
<i>Ricinus communis</i> , castor bean; seed	0.1	1	1		o	o	r					
<i>Siegesbeckia orientalis</i> , small yellow crown beard; seed	0.1	6	5			o		r				
<i>Tephrosia purpurea</i> , ahuhu; seed	0.1	13	5	o	r							

*From Ripperton and Hosaka (1942). a=abundant; c=common; o=occasional; r=rare.

†The seeds of these species are practically indistinguishable, hence they are combined herein.

TABLE 2 (Continued)
FOODS OF THE LACE-NECKED DOVE IN HAWAII

SPECIES AND PARTS EATEN	PER-CENTAGE CROP VOLUME	NUMBER OCCURRENCES IN 146 CROPS	NUMBER OCCURRENCES IN 71 GIZARDS	ABUNDANCE OF FOOD BY VEGETATION ZONE*								
				A	B	C ₁	C ₂	D ₁	D ₂	D ₃	E ₁	E ₂
PLANTS continued												
<i>Xanthium saccharatum</i> , cocklebur; seed.....	0.1	1	0	o	c	o						
Unidentified seedling.....	0.1	1	0									
<i>Abutilon molle</i> , mao; seed.....	T	5	3	r	o							
<i>Amaranthus hybridus</i> , spleen amaranth; seed.....	T	6	2		o	o						
<i>Argemone alba</i> var. <i>glauca</i> , puakala; seed.....	T	4	0	o	c							
<i>Bidens pilosa</i> , pilipili; seed.....	T	1	1	o	c	c	o	o	r			
<i>Brassica</i> sp., mustard; seed.....	T	2	0									
<i>Cassia occidentalis</i> ; seed.....	T	1	0		o	o		r				
<i>Casuarina</i> sp., ironwood; seed..	T	2	1									
<i>Chenopodium ambrosioides</i> , Mexican tea; seed.....	T	1	1		r						r	
<i>Cirsium vulgare</i> , common thistle; seed.....	T	3	3			o	c				o	
<i>Cuphea carthagenensis</i> , tarweed; seed pod.....	T	1	0			o		c	o			
<i>Dodonaea viscosa</i> , aalii; seed....	T	6	14		o	o	o				o	
<i>Echinochloa crusgalli</i> var. <i>crus-pavonis</i> , barnyard grass; seed..	T	1	0		c	c						
<i>Eleusine indica</i> , wire grass; seed..	T	1	0		r	o		r				
Fungus, puff ball.....	T	1	0									
<i>Geranium carolinianum</i> var. <i>australe</i> , wild geranium; seed..	T	1	1				c		o	o	r	
<i>Ipomoea</i> sp.; seed.....	T	1	0									
<i>Leucaena glauca</i> , koa haole; seed	T	1	0	c	a	c		o				
<i>Malva parviflora</i> , little mallow; seed.....	T	1	2		o	c	o					
<i>Malvastrum coromandelianum</i> , false mallow; pod, seed.....	T	1	1	o	c							
<i>Mimosa pudica</i> , sensitive plant; seed.....	T	1	1			o		c	r			
<i>Portulaca oleracea</i> , pigweed; seed, pod.....	T	1	0	r	o	c		o				
<i>Setaria verticillata</i> , bristly foxtail; seed.....	T	3	3	c	o	o						
<i>Sporobolus capensis</i> , rattail; seed..	T	1	2		r	o	c			o	o	
<i>Triticum aestivum</i> , wheat; seed..	T	1	0	imported			cat	tle	feed			
<i>Cassia Leschenaultiana</i> , Japanese tea; seed.....	0	0	4		c	c		r				
<i>Chenopodium oahuense</i> , aweoweo; seed.....	0	0	1		o	o					o	
<i>Desmodium uncinatum</i> , Spanish clover; seed.....	0	0	2		r	c	c	c	r		r	
<i>Indigofera suffruticosa</i> , indigo; seed	0	0	1		r	c	o	r				
<i>Paspalum Urvillei</i> , vasey grass; seed.....	0	0	1			r	r	r				
<i>Plantago</i> sp.; seed.....	0	0	1									
<i>Psidium Guajava</i> , guava; seed...	0	0	5		o	c		a	o			
<i>Styphelia Tameiameiae</i> , puakeawe; seed.....	0	0	3			o	o				o	o

TABLE 2 (Continued)
FOODS OF THE LACE-NECKED DOVE IN HAWAII

SPECIES AND PARTS EATEN	PER- CENTAGE CROP VOLUME	NUMBER OCCUR- RENCES IN 146 CROPS	NUMBER OCCUR- RENCES IN 71 GIZ- ZARDS	ABUNDANCE OF FOOD BY VEGETATION ZONE*							
				A	B	C ₁	C ₂	D ₁	D ₂	D ₃	E ₁
ANIMALS	0.5										
<i>Megacerus alternatus</i> , pea weevil; adult.....	0.2	10	0								
<i>Carpophilus humeralis</i> , yellow- shouldered souring beetle; adult.....	0.2	3	2								
<i>Carpophilus hemipterus</i> , dried fruit beetle; adult.....	0.1	3	2								
<i>Antonina graminis</i> , scale insect; fragment.....	T	2	0								
Blattidae (unidentified), cock- roach; egg case.....	T	7	0								
<i>Girphis unipuncta</i> , army worm; larva.....	T	1	0								
Coccidae (unidentified), scale insects; adult.....	T	1	0								
Coleoptera (unidentified), beetles; adult.....	T	1	0								
<i>Conoderus exsul</i> , wireworm; larva, pupa.....	T	4	0								
Crustacea (unidentified), cray- fish; chitin.....	T	1	0								
Lepidoptera (unidentified), but- terflies, moths, skippers; larva	T	1	0								
Mollusca (unidentified), aquatic snail; shell.....	T	1	0								
Rodentia (unidentified), rodent; tooth.....	T	1	0								

general distribution is only occasional in zones B and C₁, it grows very profusely during all seasons in certain areas, particularly in fallow pineapple fields and along roadsides. Lace-necked Doves show a preference for the large seeds, and concentrations of feeding birds occur where this plant is abundant and in seed.

Waltheria americana L., or uhaloa, comprising 17 per cent of the entire diet, ranks as an important food. Its seeds occurred in 57 (39 per cent) of the crops and 27 (38 per cent) of the gizzards. Uhaloa grows occasionally in zones A and C₂ but commonly in B and C₁. This exotic member of the Sterculiaceae appears to produce seeds abundantly through-

out the year. Widely available in arid sections at low elevations, this plant apparently plays a prominent role as a food in these regions where seed productivity is otherwise low. We also found uhaloa to be an important food of the Barred Dove and the California Quail (*Lophortyx californica*) in Hawaii.

Cajanus Cajan (L.) Millsp., pigeon pea, constitutes 12 per cent of the Lace-necked Doves' food. Twenty-one (14 per cent) of the crops and 4 (5 per cent) of the gizzards contained these seeds. This exotic legume is rare in zones B, C₂, and D₁, but occasional in zone C₁, where it occurs chiefly as cultivated cattle forage. Seeds are available throughout the year.

Solanum nodiflorum Jacq., or popolo, grows occasionally in zones B and D₁ but commonly in zone C₁, particularly in old pineapple fields. The fruit and seeds of this indigenous species of the Solanaceae comprised 10 per cent of the diet and occurred in 19 (13 per cent) of the crops and 11 (15 per cent) of the gizzards. Field observations show that doves often gorge themselves on these succulent fruits, which are available all year. It is possible that moisture provided by this fruit may entirely eliminate the need for surface drinking water. Popolo is also an important food of pheasants (*Phasianus torquatus* Gmelin and *P. versicolor* Veillot) in Hawaii.

Lantana Camara L. is an exotic verbena which accounted for 9 per cent of the diet.

The fruits and seeds were taken in only 7 (4 per cent) of the crops and 7 (9 per cent) of the gizzards. *Lantana* is abundant in zone B, common in C₁, and occasional in A and D₁, and this distribution makes it widely available throughout dove range. However, its relatively infrequent occurrence and small volume in the diet implies that it is not a generally preferred food. Almost the entire volume of this plant in the food analysis came from four Lace-necked Doves taken at Koloa, Kauai, in zone C₁. Two Barred Doves collected at the same place and time had also eaten large quantities of *Lantana* although it was not a common food of Barred Doves. Possibly the *Lantana* here was particularly attractive at this time or other foods may have been lack-



FIG. 5. The dense coastal stands of algaroba (*Prosopis chilensis*) furnish good roosting and nesting sites for the Lace-necked Dove. Openings as shown in the foreground support food species such as uhaloa (*Waltheria americana*), ilima (*Sida* sp.), and *Lantana Camara*. Kekaha, Kauai. Vegetation zone A, sea level; October 6, 1946.

ing. Perkins and Swezey (1934) have accredited the Lace-necked Dove with being a principal agent in the wide dissemination of *Lantana* throughout coastal areas. However, the limited feeding on *Lantana* and the fact that all *Lantana* seeds in gizzards were ground up indicates to us that Lace-necked Doves may have contributed little to the spread of this noxious shrub. Probably of greater importance in permitting its spread in the Islands was the lack of natural checks on this exotic plant in its new environment.

The seeds and fruits of *Wikstroemia phillyraefolia* Gray, locally known as akia, were utilized by Lace-necked Doves as 4 per cent of the diet. They occurred in 5 (3 per cent) of the crops and 3 (4 per cent) of the gizzards. The small volume and rare occurrence in the diet are probably related to the distribution of akia, which is rare in zone B and occasional in C₁. However, on certain lava outcrops in zone C₂ on Hawaii, this endemic species of the Thymelaeaceae is abundant and is believed to be a preferred food because of its intensive utilization by Lace-necked Doves there. The fruits of this plant, too, furnish a ready supply of moisture. Akia, obtainable during all seasons but most abundantly during spring, summer, and fall, also ranks as an important food of pheasants and feral pigeons (*Columba livia* Gmelin) in Hawaii.

Portulaca sclerocarpa Gray, or ihmakole, formed 3 per cent of the food of Lace-necked Doves. It occurred in 17 (11 per cent) of the crops but in no gizzards. Both seed pods and seeds of this endemic species of the Portulacaceae are fed upon in zone B, where it occurs rarely.

Dianella sandwicensis Hook. and Arn., or ukiuki, grows occasionally in zones D₁ and D₂. The crop and gizzard of only one bird contained seeds and fruits of this plant, which amounted to 3 per cent of the total foods. This bird was taken from zone D₃ at Kokee, Kauai, where the ukiuki fruits abundantly during summer and fall. Doves in this section

have been observed to feed upon the seeds and fruits of this species but because of its limited distribution and the scarcity of Lace-necked Doves in this zone, it cannot be considered a major food. This endemic lily is an important food of pheasants and Jungle Fowls (*Gallus gallus* (L.)) in this area.

Sida cordifolia L. and *Sida fallax* Walpers, both called ilima, are indigenous species of the family Malvaceae. Because their seeds are practically indistinguishable, their utilization has been combined as 2 per cent of the Lace-necked Doves' food. These plants occurred in 32 (21 per cent) of the crops and 10 (14 per cent) of the gizzards. The former species is occasional in zone A, common in B, and rare in C₁, while the latter is common in zones A and C₁ and abundant in B. These species produce seeds abundantly throughout the year although during some drouth periods production is slackened. They, combined with uhaloa, provide a desirable combination of foods in drier and more barren parts of dove range.

The remaining plant and animal foods appear to be of less importance because of their small volumes and the infrequencies of their occurrence in the diet. However, as contributions to variety and to nutrition they are doubtless of value. Most plants in this group are widely available in areas from which birds were collected. In many parts of the range there is apparently sufficient food to support higher dove populations than now exist.

Grit occurred in 17 crops and 38 gizzards and averaged 0.3 cubic centimeter in both cases; 10 additional gizzards had traces of grit while 23 had none. Both angular and well-rounded pieces of feldspar, olivine, basalt, quartz, bottle glass, opaline, and round concretions of hard earth, from 1 to 4 millimeters in diameter, were found.

FEEDING, WATERING, AND ROOSTING HABITS

Feeding is occasional from an hour or more after daylight until about noon, when it is

greatly accelerated. In those areas of abundant food far removed from roosting sites, Lace-necked Doves infiltrate irregularly throughout the morning, reaching an apparent maximum number about noon. Heaviest feeding takes place during the next few hours. Beginning about 3:00 P.M. birds with full crops (averaging 10.1 cubic centimeters in 85 birds with a maximum of 35.1 cubic centimeters) start returning singly or in groups of twos or threes along definite flyways to their roosting sites. Distances of at least 5 miles are often traveled between feeding grounds and communal, coastal roosting sites but doves may reside in certain roosting areas with available food.

Lace-necked Doves and Barred Doves often feed in the same fields, giving rise to the local opinion that serious competition for foods occurs between these species. However, Lace-necked Doves select principally large seeds and fruits while Barred Doves utilize small-seeded, rapidly maturing annuals and grasses (Schwartz and Schwartz, 1949). As a result of these food preferences, the use of these fields by each species is generally at different stages of cultivation or plant succession. Although some of the foods eaten by both doves may be of the same species, it is highly significant that only one plant, uhaloa, is an important food in the diet of both birds. This shrub occurs in great abundance throughout most dove range and the seeds are more than ample to supply the needs of both species of doves as well as of other game birds which also utilize them.

Our observations indicate that either fresh or brackish surface water or succulent fruit is a prerequisite for good Lace-necked Dove range. Birds resident in areas without available surface water appear to substitute succulent fruits in fulfilling their daily water needs. Elsewhere, doves readily utilize cattle troughs (especially overflow or seeps), irrigation ditches, reservoirs, pools, streams, and springs, in addition to rainfall and dew which may collect in the leaf axils of many

plants. The proximity of these water sources to feeding and roosting areas plays an important role in the daily range. Customarily, Lace-necked Doves use water close to their feeding area in late afternoon but in the morning resort to a water source near their roosts. At these latter sites they may linger and bathe and preen their feathers before venturing out to their foraging grounds for the day. In some dry sections, existing water holes now attract doves over approximately a 5-mile radius. The presence of water within flying range of the nest has been shown by Arnold (1943) to be a necessity for the western White-winged Dove, *Zenaida asiatica mearnsi* (Ridgway), and it is not unlikely that a similar requirement holds for the Lace-necked Dove in Hawaii.

Roosting areas are usually dense wooded thickets of algaroba on the coastal flats, dense groves of *Eucalyptus* sp. or of ironwood (*Casuarina* sp.), or the peripheries of forested areas and wooded draws radiating therefrom, although some roosting occurs in practically any timbered area. In some parts of the Islands, Lace-necked Doves tend to be gregarious in their roosting habits, and the commonest community roosting sites in the dense coastal stands of algaroba harbor nightly populations of a hundred or more birds per acre.

BREEDING

From the little evidence accumulated during this survey, we believe that Lace-necked Doves breed mostly from February through September and possibly, to a limited extent, during the entire year.

We noticed that the "cooing" song of the males becomes greatly accelerated during January and for the next 2 months is increasingly obvious during the early morning hours and to a lesser extent during the day. After a peak from mid-March through mid-July, the intensity of "cooing" in the general population gradually diminishes until by late October occasional courting songs are heard

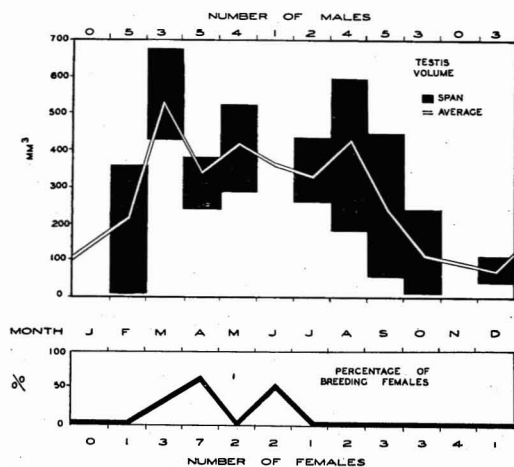


FIG. 6. Breeding of the Lace-necked Dove in Hawaii.

only in early morning. These variations in vocal activity generally coincide with fluctuations in testis volumes (roughly computed by multiplying length \times width \times depth of both testes per individual) of 35 collected adult males, and with indications of breeding (determined by the presence of maturing Graafian follicles) in 29 collected adult females (Figure 6). We do not believe that breeding is common after September, as evidenced by the fact that 86 birds collected from October through December all were in adult plumage.

In southern China, the breeding season of the species *S. chinensis* is spring, summer, and autumn (La Touche, 1931-34) and in India these doves are reported to breed throughout the year (Ali, 1944) and probably to raise several broods annually (Whistler, 1935). Breeding of this species in the Malay Peninsula generally extends from January to March, but extremes from November to May occur (Robinson and Chasen, 1936).

In Hawaii, the Lace-necked Dove shows a wide selection of nesting sites. Typical ones observed during this survey are as follows: (1) in a strong crotch 10 feet above the ground in an algaroba tree; (2) 35 feet above the ground in the outer branches of an algaroba tree; (3) in a clump of cactus (*Opuntia megacantha*) on a sloping stem 6 feet above



FIG. 7. A Lace-necked Dove nest in puakeawe (*Styphelia Tameiameiae*). Kapapala, Hawaii. Vegetation zone C₂, elevation 4,000 feet; June 8, 1946.

the ground; (4) in a thicket of *Smilax* sp. and akala (*Rubus hawaiiensis*) growing on the rim of a gulch 25 feet deep; (5) 18 feet above the ground in the outer fringes of a mamani tree (*Sophora chrysophylla*); (6) 5 feet above the ground in a puakeawe bush (*Styphelia Tameiameiae*); (7) 35 feet above the ground in the outer branches of an ironwood tree.

The nest is typically dove-like, consisting



FIG. 8. Juvenile Lace-necked Dove. Note the lack of the neck "lace" so characteristic of the adult. Honolulu, Oahu. Sea level; May 15, 1946.

of a flimsy platform about 7 inches in diameter, roughly constructed of twigs between 1/8 and 1/4 inch in diameter and about 4 or 5 inches long. Sometimes it contains a lining of fine rootlets for the two white eggs.

The juvenile plumage lacks the black and white neck "lace" so characteristic of the adult, and the contour feathers are distinctly and narrowly light-tipped. Three nest-free birds in juvenile plumage had bursae of Fabricius 4 to 5 millimeters in length. Thirteen birds in adult plumage had no measurable bursae while two others had bursae measuring 3 and 5 millimeters, respectively. Riddle (1928), working with other species of *Streptopelia*, found that bursae usually, but not invariably, involuted at sexual maturity.

SEX RATIOS, WEIGHTS, AND MEASUREMENTS

Sex ratios found in the Lace-necked Dove in Hawaii are as follows:

	NUMBER OF MALES	NUMBER OF FEMALES	MALES PER 100 FEMALES
79 adult and nest-free juvenile doves.....	43	36	119:100
64 adults.....	35	29	120:100
15 juveniles.....	8	7	114:100

Three adult males averaged 146 grams and three adult females averaged 159 grams in weight. This small series indicates that females may be heavier than males. However, measurements of 59 adult Lace-necked Doves show males to be slightly larger than females (Table 3).

PARASITES

Lice were the only external parasites observed on Lace-necked Doves and infestations

were light to moderate. *Goniodes* sp. larvae, *Goniodes chinensis* Kell. & Chap., and a new species of *Columbicola*, not yet described, occurred on collected birds. The latter two species were also identified from Barred Doves in Hawaii.

Intestinal roundworms, *Ascaridia columbae* (Gmelin), were found occasionally, thus establishing a new host record for this parasite. *A. columbae* also occurred in feral pigeons in Hawaii. We found the eyeworm, *Oxyspirura mansoni* Cobbold, in Lace-necked Doves, as did Alicata (1947), and in the Japanese Quail (*Coturnix coturnix japonica* Temminck and Schlegel), and in pheasants in Hawaii. The heaviest infestation was two worms in each eye of a single dove. *Subulura brumpti* (Lopez Neyra), a cecal roundworm, occurred in a single specimen. This parasite is common in Japanese Quail and pheasants in Hawaii. Known intermediate hosts of the latter two

parasites were not found in this food habits study, but doubtless are consumed by the Lace-necked Dove.

The cestode *Davainea crassula* (Rudolphi) was found in the Lace-necked Dove; this is another new host record. It also occurred in feral pigeons in Hawaii. Infestations varied from light to extremely heavy. The intermediate host of this parasite is unknown but since the diet of Lace-necked Doves includes some insects and mollusks, it is possible that

TABLE 3
AVERAGE MEASUREMENTS IN MILLIMETERS OF 59 ADULT LACE-NECKED DOVES

MEASUREMENTS	33 ADULT MALES	26 ADULT FEMALES
Total length.....	324.0	318.4
Extent of wing.....	459.4	451.0
Length of closed wing.....	152.4	150.0
Length of tail.....	145.6	141.5
Exposed culmen.....	17.4	16.8
Length of middle toe including nail.....	25.4	25.3

infestations with this cestode may occur as a result of consumption of these food forms.

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SUMMARY

1. Lace-necked Doves (*Streptopelia chinensis chinensis*) are permanent residents on all of the major Hawaiian Islands. A total of 3,120 square miles is occupied by an estimated 88,680 Lace-necked Doves with densities varying from less than 10 to 200 birds per square mile. The range occurs mostly from sea level to 4,000 feet elevation but in one area on Hawaii it reaches 8,000 feet. All types of land except dense forests and barren lava support doves. The optimum range occurs from sea level to 2,500 feet elevation. Here, the mean annual temperature is between 75° and 70° F. and extremes in the annual rainfall are from less than 10 to approximately 60 inches. Where rainfall is greater and/or temperatures lower, lesser populations occur.
2. An analysis of foods in 146 crops shows that 65 plant species comprise 99.5 per cent of the diet while 13 animal items constitute the remaining 0.5 per cent. Of the plant matter, seeds and pods amount to 84.1 per cent, succulent fruits 14.4 per cent, and roots and seedlings 1.0 per cent. Grit occurred in 17 crops and 38 gizzards, averaging 0.3 cubic centimeter in each case. Feeding activity is greatest from approximately noon to 3:00 P.M. No competition for food occurs between Lace-necked and Barred Doves in Hawaii.
3. Either fresh or brackish surface water or succulent fruit is a prerequisite for good Lace-necked Dove range.
4. Lace-necked Doves may fly as far as 5 miles between roosting and feeding areas but favorable sites with both available food and good roosting cover have resident populations.
5. Roosting areas are usually densely wooded thickets along the coastal flats, occasional dense groves, or the peripheries of forested areas and wooded draws radiating therefrom, but some roosting occurs in practically any timbered area.
6. Lace-necked Doves breed mostly from February through September and pos-

sibly to a limited extent during the entire year.

7. The juvenile plumage lacks the black and white neck "lace" so characteristic of the adult and contour feathers are distinctly light tipped.
8. The sex ratio in 79 adult and nest-free juvenile doves was 43 males to 36 females or 119:100. Weights of 6 adults and measurements of 59 adults are given.
9. Lice externally and roundworms in the intestine, eye, and caecum occurred generally in light infestations. Tapeworm parasitism varied from light to extremely heavy.

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